The response of carbon assimilation and storage to longterm drought in tropical trees is dependent on light availability

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RESEARCH ARTICLE

The response of carbon assimilation and storage to long-term drought in tropical trees is dependent on light availability

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Abstract

1. Whether tropical trees acclimate to long-term drought stress remains unclear. This uncertainty is amplified if drought stress is accompanied by changes in other drivers such as the increases in canopy light exposure that might be induced by tree mortality or other disturbances.
2. Photosynthetic capacity, leaf respiration, non-structural carbohydrate (NSC) storage and stomatal conductance were measured on 162 trees at the world's longest running (15 years) tropical forest drought experiment. We test whether surviving trees have altered strategies for carbon storage and carbon use in the drier and elevated light conditions present following drought-related tree mortality.
3. Relative to control trees, the surviving trees experiencing the drought treatment showed functional responses including: (a) moderately reduced photosynthetic capacity; (b) increased total leaf NSC; and (c) a switch from starch to soluble sugars as the main store of branch NSC. This contrasts with earlier findings at this experiment of no change in photosynthetic capacity or NSC storage. The changes detected here only occurred in the subset of drought-stressed trees with canopies exposed to high radiation and were absent in trees with less-exposed canopies and also in the community average. In contrast to previous results acquired through less intensive species sampling from this experiment, we also observe no species-average drought-induced change in leaf respiration.
4. Our results suggest that long-term responses to drought stress are strongly influenced by a tree's full-canopy light environment and therefore that disturbance-induced

changes in stand density and dynamics are likely to substantially impact tropical forest responses to climate change. We also demonstrate that, while challenging, intensive sampling is essential in tropical forests to avoid sampling biases caused by limited taxonomic coverage.

KEYWORDS

drought, leaf respiration, light, non-structural carbohydrate, photosynthesis, stomatal conductance, tropical forest

1 | INTRODUCTION

Continued rises in atmospheric CO_2 concentration are likely to increase atmospheric temperature and potentially decrease atmospheric humidity, which may lead to substantial long-term soil moisture deficit for tropical trees (Marengo et al., 2018). Long-term drought stress is likely to result in increased tree mortality (Allen et al., 2015), particularly in the largest tree size classes (da Costa et al., 2010; Stovall et al., 2019) or in greater leaf loss, depending on the species (Wolfe et al., 2016). These changes are very likely to reduce competition for light and water, but may also exacerbate any existing drought stress through increased leaf and canopy temperatures, via increased radiation loads. Exploring the combined impacts of drought and elevated light availability on leaf functional traits relating to carbon assimilation, storage and use is essential to predicting long-term drought responses by tropical forest trees.

1.1 | Impacts of drought on plant function

Studies have shown that drought stress usually reduces photosynthetic assimilation, carbon storage in the form of non-structural carbohydrate (NSC) concentration and plant respiration rates (e.g. Atkin & Macherel, 2009; Klein et al., 2014; Sevanto et al., 2014), though there have been some reports for crops and forest trees where respiration has increased under drought (Atkin & Macherel, 2009; Miranda et al., 2005). In general, though, over long time-periods, a downregulation of key controls on photosynthetic capacity (maximum carboxylation capacity, V_{cmax} and maximum electron transport, J_{max}) would be expected if the metabolic cost of their maintenance outweighs the overall gains. However, counter to this expectation, previous studies at a long-term tropical forest drought experiment demonstrated no significant average long-term change in V_{cmax} or J_{max}, or in NSC storage in response to drought (Rowland, da Costa, Galbraith, et al., 2015; Rowland, Lobo-do-Vale, et al., 2015), although increases in leaf, stem and root respiration were reported (Meir et al., 2018; Metcalfe, Lobo-do-Vale, et al., 2010; Rowland, Lobo-do-Vale, et al., 2015; Rowland et al., 2018). These results suggested that functional responses to aid survival in this drought experiment may be larger for certain traits and fluxes related to carbon cycling than for others (Meir et al., 2018; Rowland, Lobo-do-Vale, et al., 2015). However, rainfall exclusion studies such as this do not simulate compounding influence of joint atmospheric and soil drought (Meir et al., 2015). Furthermore, previous analyses did not focus on the combined effects of tree size and related variation in full-canopy light exposure following mortality during the extended soil moisture deficit treatment and because of resource constraints the sampling could not cover a large number of genera (six) that exhibited contrasting mortality responses to drought (Meir et al., 2018; Rowland, da Costa, Galbraith, et al., 2015).

Carbon assimilation and storage of a plant are normally assumed to be controlled by changes in the environment, inducing differences in carbon supply (photosynthesis), which then drive subsequent changes in carbon use (growth and respiration) and NSC storage (Mooney, 1972). Currently however, there is conflicting evidence as to whether NSC storage increases, decreases or remains the same in trees during drought. Following extended drought, reduced growth or other carbon use restrictions may result in little change or even increases in overall NSC stores during drought, including wet-dry seasonal cycles (e.g. Klein et al., 2014; Sala & Hoch, 2009; Würth et al., 2005), partcularly in tropical tree species (Adams et al., 2017). In contrast, strong declines in NSC have been observed (e.g. Galiano et al., 2010), principally during extreme or extended drought, with the potential for associated mortality (Mitchell et al., 2013). Consequently, the adjustments in different NSC stores during periods of environmental stress, such as prolonged drought or changes in light availability, result from changes in carbon assimilation and use that reflect different ecological responses.

1.2 | Impacts of changing light environment on plant function

The light environment exerts strong controls on photosynthesis, assuming trees also tend to optimise photosynthesis in relation to available light and nutrients as they grow within a canopy (Field & Mooney, 1986; Kull & Kruijt, 1999). Partial acclimation to light has been demonstrated by observations of near-linear increases in relative leaf gas exchange capacity and relative incident irradiance within the vertical profile of forest canopies, both tropical and non-tropical (Domingues et al., 2007; Meir et al., 2002), and by changes in predicted and measured NSC concentrations and photosynthetic capacity with irradiance (Kull & Kruijt, 1999; Li et al., 2016). Whether a plant will increase total carbon assimilation, carbon storage and carbon use in response to elevated light will depend on the degree of additional

stress it suffers due to the elevated temperatures and vapour pressure deficits (VPD) that are likely to accompany such changes. For example, if the CO_2 concentration in the leaf becomes lower as a consequence of reduced stomatal conductance (g_s) in response to higher temperatures (or indeed low leaf water potential), a plant may increase photosynthetic capacity to compensate for the reduction in g_s, or downregulated in order to prevent further water loss (Wang et al., 2017). Therefore it is possible that elevated radiation may act to restrict photosynthesis, causing photosynthetic capacity to depart from the optimal values that would be reached by full acclimation solely in response to a given radiation load (Meir et al., 2002).

1.3 | The Caxiuanã drought experiment

This study follows 15 years of research from a large-scale drought experiment situated in the National Forest Reserve of Caxiuanã, Pará State, Brazil. The drought treatment was initiated in 2002, when 50% of the incoming through-fall over a 1-ha area was excluded. Studies at this site compared this droughted treatment with an equally sized, non-droughted, control treatment (see Meir et al., 2018, for experimental details and principal results). Initially the forest demonstrated resistance to the drought in terms of tree mortality (da Costa et al., 2010). However, after 3 years, tree mortality rates began to increase, with the highest mortality increases observed in the largest tree size class (da Costa et al., 2010; Meir et al., 2015), leading to a 40% reduction in above-ground biomass by 2015 (Rowland, da Costa, Galbraith, et al., 2015). The mortality of the large trees increased exposure to light for the lower canopy trees, increasing the average growth rates of small to medium understorey trees (Metcalfe, Lobo-do-Vale, et al., 2010; Rowland, da Costa, Galbraith, et al., 2015). These elevated growth rates were not associated with changes in photosynthetic capacity between the droughted trees and corresponding non-droughted trees (da Costa et al., 2010; Rowland, Lobo-do-Vale, et al., 2015), however, they did occur alongside significant increases, relative to the non-droughted trees, in the respiration rates in leaves and woody tissue of the sampled droughted trees (Metcalfe, Lobo-do-Vale, et al., 2010; Metcalfe, Meir, et al., 2010; Rowland, Lobo-do-Vale, et al., 2015). Critically, to date none of the studies on this experiment has explored the interacting effects of light and drought, as work has either focused on: (a) the large fully sunlit canopy trees of two subsets of genera that demonstrated contrasting mortality responses to the drought treatment (da Costa et al., 2010); or (b) has separated out trees into stem size classes rather than by the amount of incident radiation their canopies receive.

Here we explore the combined impact of long-term (15 year) drought stress and changes in light availability at the world's longest running drought experiment located in tropical forest. We use this experiment to study trees in high- and low light environments located on the drought treatment and a corresponding control treatment. We test the following hypotheses.

1. Plant functional traits associated with carbon assimilation, use and storage are downregulated following long-term drought stress.
2. Adjustments in the functional traits controlling assimilation, use and storage of carbon during drought are significantly affected by overall light availability to the crown of a tree.
3. Taxonomic identity is associated with significant variations in the relationships among carbon assimilation, its use and storage, in addition to changes in light availability and drought stress.

2 | MATERIALS AND METHODS

2.1 | Site and tree selection

Our study was performed on a through-fall exclusion experiment located in the Caxiuanã National Forest Reserve, north-east Brazil (1°43′S, 51°27W). The site is a terra firme lowland tropical evergreen forest, receiving on average 2,000–2,500 mm rainfall per year, with a pronounced dry season which occurs between June and November. The drought treatment is on a 1-ha forest plot, on which plastic panels installed at the height of 1–2 m have been used to exclude 50% of the incoming canopy through-fall since 2002, for the 15 years before this study took place, in 2016. Additional experimental details can be found in previous publications (e.g., da Costa et al., 2010; Meir et al., 2015; Rowland, da Costa, Galbraith, et al., 2015).

We selected 162 trees, 86 from the control forest and 76 from the drought treatment, taken from the 12 most common genera, and which had replicates of trees on both the treatment and control forest (see Table S1 for full details of trees sampled). Within the selected genera we sampled tree diameters from 10 cm to 89 cm diameter at breast height, (diameter at 1.3 m height; DBH) to capture a large range of tree crown exposure to light. At the time of sampling each tree was given a light class score to reflect the quantity of incident radiation the whole canopy receives. The canopy exposure scores consisted of: 1—fully shaded tree, receiving no direct sunlight; 2—non-canopy top tree which has a large majority of shaded leaves; 3—non-canopy top tree which has sunlit leaves in the upper branches, but still has a large proportion of shaded leaves; 4—canopy top tree with full canopy illumination; 5—canopy emergent tree (crown extending well above main canopy height – 35 to 40+ m), or tree located in a large canopy gap with full canopy illumination. The light-class estimation was performed repeatedly and independently by two people. We subsequently grouped trees into high light-exposed tree canopies (classes 4 and 5) and lower light-exposed tree canopies (classes 2 and 3) for analysis. Class 1 was not included in these groupings for treatment comparisons as these trees were rare on the drought treatment ($n = 2$).

2.2 | Trait sampling

A branch ~1 m in length was harvested from each tree between 09:00 and 10:00, in peak dry season (16 September 2016 and 01 October

2016), although on occasions (<5%), where this was not possible, the remaining samples were cut before 13:00. These branches were re-cut in a bucket of water in a canopy gap on the forest floor. Once leaf conditions had stabilised an A-C_i curve was measured with a Li-COR 6400 portable photosynthesis system (Li-COR), from which photosynthetic capacity parameters (V_{cmax} and J_{max}) were derived. On a leaf adjacent to the one on which the A-C_i curve was determined, leaf respiration in the dark (R_{leaf}) was measured. A leaf was covered in aluminium foil and left in the dark for a minimum of 30 min, before gas exchange was measured. The maximum g_s obtained during the A-C_i curve (usually at the lowest CO_2 level) was recorded. Minimum g_s was taken as the g_s value measured when maximum stomatal closure had occurred and at the end of the R_{leaf} measurement. Full protocols for each gas-exchange measurement are available in the Supplementary Methods.

The leaves on which the A-C_i curve and R_{leaf} were measured were cut off at the petiole following the gas exchange measurements and placed in a humid zip-lock plastic bag. These leaves were used to measure leaf mass per area (LMA, g/m^2), leaf nitrogen and leaf phosphorus (see Supplementary Methods).

Using the branches sampled for gas exchange, wood samples ~1 cm in diameter and 10 cm in length were taken together with 3–20 leaves (depending on leaf size) and used for the measurement of NSC. NSC samples were processed and dried in the field and then transported to a laboratory where soluble sugars and starches were analysed (see Supplementary Methods).

2.3 | Data analyses

Analysis was performed in R (R.3.4.2, R Core Team) using individual tree-level data. We first focused on determining if the traits related to carbon assimilation, use and storage were altered under drought, and then if changes were observed, whether they were influenced by light availability, independently of taxon. We first divided tree trait data into low and high light categories (see above) separated by drought and control trees. A Wilcoxon rank-sum test was then used to test for significant differences between categories. We note that this analysis assumes that each tree can be treated as an independent random sample, with light and drought, rather than taxon, controlling the majority of variance in our measured variables. Consequently we go on to evaluate the role that taxon plays in controlling the drought and light responses in our experiment using mixed effect models (MEM). Mixed effect models were performed using the LME4 package (Bates et al., 2015), separately for high and low light classes and for each trait using treatment (control and treatment) as a fixed variable. Genus was always retained as a random effect in each model, however, 3 of the 12 genera (*Micropholis*, *Syzygiopsis*, *Virola*), had <5 replicates on either the control plot or treatment plot and so were grouped into one general taxon group. All trait data used in the MEM were log transformed and each model was tested for non-constant error variance using the *check_heteroscedasticity* function from the PERFORMANCE package (Lüdecke et al., 2020) and only reported if the error variance was homoscedastic. Significance values for the fixed factor were derived using the LMERTEST (Kuznetsova et al., 2017) and we calculated both the marginal and conditional coefficient of determination (r^2, Nakagawa & Schielzeth, 2013). The code for this MEM analysis is provided in the supplemental material. Further exploratory analysis was done to elucidate the role taxonomy played in our results by exploring the trait variance which existed both within genera and within species.

We then tested for variations in relationships between light class and the log transformed gas exchange parameters between droughted and non-droughted trees. To do this analysis we treated all light classes (classes 1–5) as an ordered factor and related them to gas exchange parameters in a generalised linear model (glm). With an ordered factor a glm tests for linear, quadratic, cubed and x^4 relationships between the continuous dependent variable (gas exchange parameters) and the dependent variable (ordered factor). Finally, standardised major axis regression (SMA, SMATR package, Warton et al., 2012) was used to test for the scaling of slopes and intercepts in the relationships between specific pairs of measured variables. These bi-variate plots allowed us to test if relationships between traits varied between the control and drought treatment. In a second analysis, we tested whether the scaling between gas-exchange parameters and our other leaf traits (e.g. LMA) differed across control and treatment treatments as well as between trees of low and high light classes. All data are presented as mean values for treatment (control and treatment), or treatment and light-class, with the error shown as the *SE* of the mean.

3 | RESULTS

When trees were divided into high (4–5) and low (2–3) light classes there was a significant reduction in V_{cmax} and J_{max} in the treatment (i.e. droughted) trees relative to the control trees within the high light class (Figure 1a,b, $p < 0.05$, Wilcoxon test). However, no significant differences between the drought treatment and control were found in the lower light class trees, or when trees in all light classes were combined (data not shown). Light class also strongly influenced the differences in NSC concentrations between the control and the treatment trees. We found no significant differences in NSC storage between the control and the treatment trees for soluble sugars, starch or total NSC concentrations for trees in the low light class category (tree light score 2–3, Figure 2a,c). However, in the high light class category (tree light score 4–5) we found soluble sugars in the branches significantly increased (Figure 2d $p < 0.01$, Wilcoxon test), as did starch in the leaves (Figure 2b, $p = 0.03$, Wilcoxon test). In contrast starch in the branches significantly decreased (Figure 2d, $p < 0.05$, Wilcoxon test), for the treatment trees relative to the control trees. The increase in soluble sugars and decline in starch in the branches of the treatment trees in the high light category led to no significant change in the total branch NSC concentration. In contrast, the increase in starch in the leaves in the high light class drought treatment trees led to a significant ($p < 0.05$, Wilcoxon test) increase of total leaf NSC in the high light class drought treatment trees relative to the corresponding control

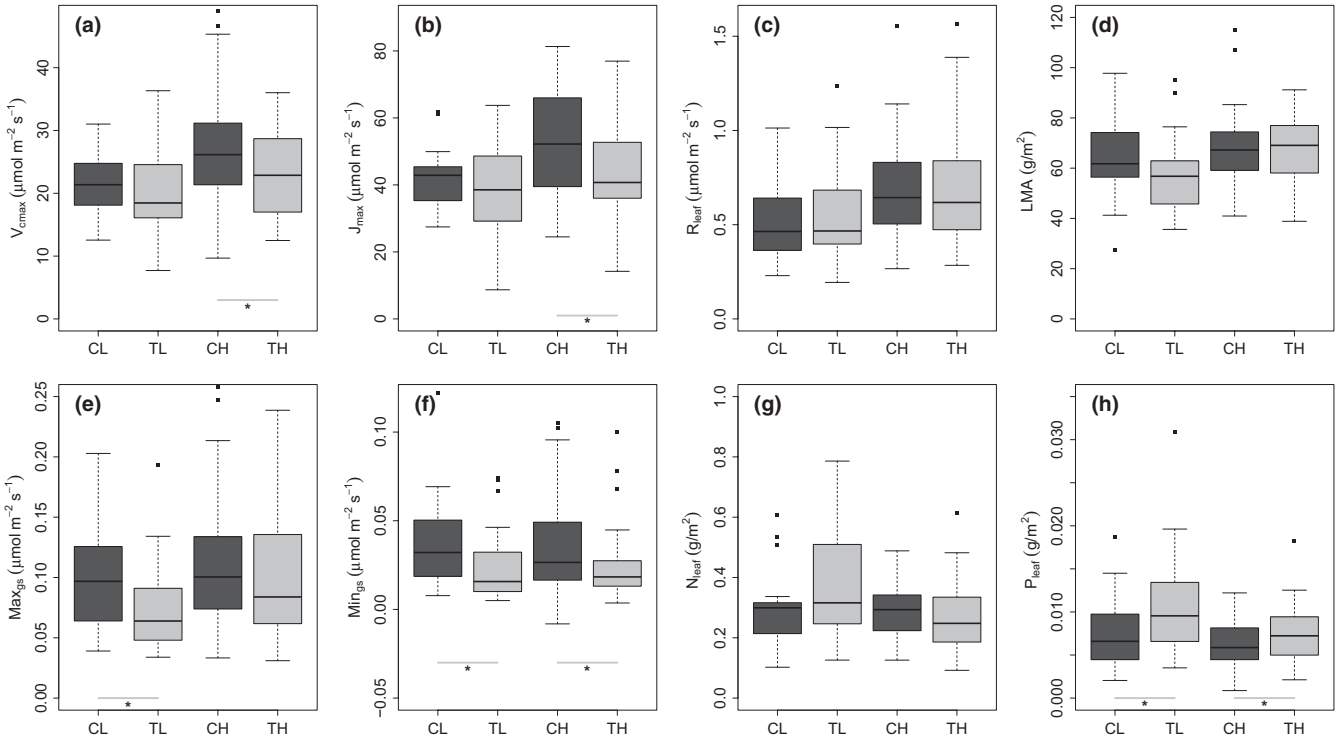
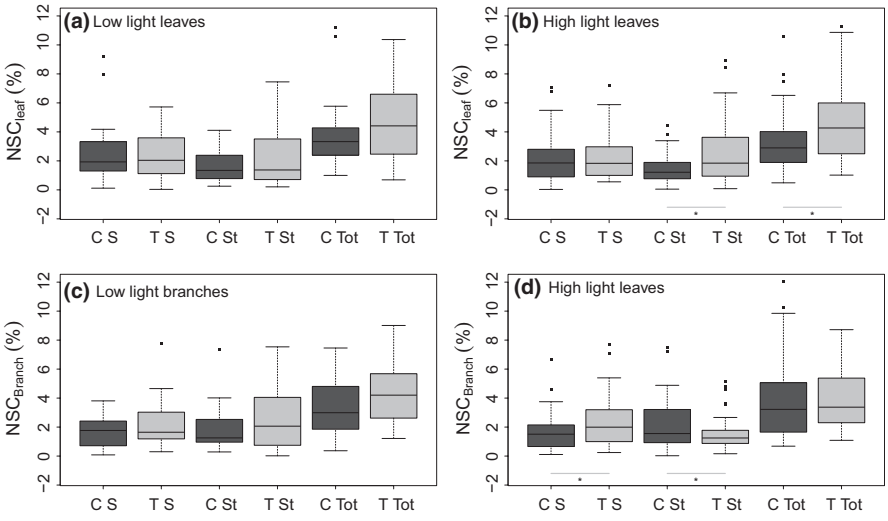


FIGURE 1 Box plots of variables for the control trees (C, dark grey) and drought treatment trees (T, light grey) treatments separated by light classes grouped into classes 2–3 (low light environments, L) and 4–5 (high light environments, H), including: (a) Maximum carboxylation capacity (V_{cmax}, μmol m^{-2} s^{-1}), (b) Maximum electron transport rate (J_{max}, μmol m^{-2} s^{-1}), (c) Leaf dark respiration (R_{leaf}, μmol m^{-2} s^{-1}), (d) Leaf mass per area (LMA, g/m^2), (e) Maximum stomatal conductance (g_s, mmol m^{-2} s^{-1}), (f) Minimum stomatal conductance (g_s, mmol m^{-2} s^{-1}), (g) Leaf nitrogen concentration (N_{leaf}, g/m^2), (h) Leaf phosphorus concentration (P_{leaf}, g/m^2). *Under grey lines indicate significant differences between box plots at $p < 0.05$ tested using Wilcox rank-sum test. Note that light class 1 is not included in this analysis as only two light class 1 trees were observed on the treatment, relative to 17 in the control plot. Sample sizes for each bar are shown in Table S2

FIGURE 2 Box plots of non-structural carbohydrate concentrations (NSC, %), including soluble sugars (S), starch (St) and total NSC concentration (Tot) for leaves (a, b) and branches (c, d) for the control (C, dark grey) and drought treatment (T, light grey) trees from low light (classes 2–3) (a, c) and high light (classes 4–5) (b, d). *Under grey lines indicate significant differences between the control and drought treatment trees for each pair at $p < 0.05$ tested using Wilcoxon rank-sum test. Sample sizes for each bar are shown in Table S2



trees. However, the effect of light may be confounded by the influence of the drought treatment or other factors, controlling intra- or interspecific variability, as no significant influence of light was indicated by the MEM results (Table 1; Table S3). No significant differences between the control and drought treatment trees were found in either light class for R_{leaf}, LMA or N_{leaf} (Figure 1c–e,k). Minimum g_s was lower on the treatment across both the low and high light classes (Figure 1f, $p = 0.03$ and 0.02 respectively, Wilcoxon test). In contrast P_{leaf} was significantly higher ($p < 0.05$, Wilcoxon test) across both light classes on the drought treatment relative to the control (Figure 1k, Wilcoxon test). However, few significant relationships between measured leaf gas exchange metrics (photosynthetic capacity and leaf respiration) and physiochemical leaf traits were found on either treatment (Figure S1).

TABLE 1 Parameter estimations from mixed effect models testing the role of drought treatment (treatment relative to control) for trees separated into High (classes 4–5) and Low (classes 2–3) on maximum carboxylation capacity (V_{cmax}, μmol m^{-2} s^{-1}), maximum electron transport rate (J_{max}, μmol m^{-2} s^{-1}), leaf mass per area (LMA, g/m^2), minimum stomatal conductance (g_s, mmol m^{-2} s^{-1}), leaf nitrogen concentration (N_{leaf}, g/m^2), leaf phosphorus concentration (P_{leaf}, g/m^2) and non-structural carbohydrate concentrations (NSC, %), including soluble sugars (S), starch (St) and total NSC concentration (T_NSC) for leaves and branches. We show the coefficient values for the intercept and fixed factor (plot), alongside the *SE* on this term and the significance value (*p*) of these values. The proportional contribution of the variance due to the random variable genus is shown. The marginal (including only fixed variables) and conditional R^2 (including fixed and random variables) are reported. We note species nested within genus did not contribute more than genus alone to any model and so these results are not shown here. Models with a significant fixed treatment effect are shown shaded in grey and in bold. To highlight how these results match with those in Figures 1 and 2 we have put black boxes round the models where the treatment effect was visible in these figures. Note all data were logged for this analysis to eliminate model heteroscedasticity

		Intercept			Fixed treatment effect					
Trait	Light class	Coefficient	*SE*	*p*	Coefficient	*SE*	*p*	Random Var. %	Marginal r^2	Conditional r^2
V_{cmax}	High	**3.25**	**0.06**	**0.00**	**−0.15**	**0.07**	**0.03**	**14.57**	**0.05**	**0.15**
	Low	3.05	0.06	0.00	−0.08	0.09	0.39	1.56	0.02	0.02
J_{max}	High	**3.89**	**0.07**	**0.00**	**−0.13**	**0.07**	**0.05**	**22.19**	**0.04**	**0.22**
	Low	3.70	0.08	0.00	−0.14	0.09	0.15	19.30	0.04	0.19
R_{leaf}	High	−4.57	0.06	0.00	−0.02	0.08	0.78	0.00	0.00	0.00
	Low	−0.65	0.11	0.00	0.01	0.13	0.93	14.00	0.00	0.14
LMA	High	4.20	0.05	0.00	0.02	0.05	0.67	24.91	0.00	0.25
	Low	4.10	0.06	0.00	−0.09	0.07	0.25	6.31	0.03	0.06
Max g_s	High	−2.31	0.09	0.00	−0.14	0.12	0.25	5.89	0.02	0.06
	Low	**−2.36**	**0.10**	**0.00**	**−0.34**	**0.13**	**0.01**	**14.86**	**0.12**	**0.15**
Min g_s	High	**−3.60**	**0.16**	**0.00**	**−0.35**	**0.18**	**0.05**	**14.95**	**0.04**	**0.15**
	Low	**−3.51**	**0.15**	**0.00**	**−0.51**	**0.20**	**0.02**	**13.38**	**0.11**	**0.13**
N_{leaf}	High	2.91	0.07	0.00	−0.07	0.06	0.24	38.03	0.01	0.38
	Low	2.84	0.08	0.00	0.07	0.08	0.40	30.68	0.02	0.31
P_{leaf}	High	**−1.04**	**0.09**	**0.00**	**0.25**	**0.09**	**0.01**	**23.94**	**0.08**	**0.24**
	Low	**−0.92**	**0.09**	**0.00**	**0.25**	**0.11**	**0.03**	**17.29**	**0.10**	**0.17**
S_{branch}	High	**0.18**	**0.12**	**0.15**	**0.45**	**0.17**	**0.01**	**7.55**	**0.08**	**0.08**
	Low	0.23	0.18	0.21	0.36	0.25	0.15	4.60	0.05	0.05
St_{branch}	High	0.48	0.15	0.00	−0.34	0.21	0.11	3.08	0.03	0.03
	Low	0.34	0.23	0.16	0.01	0.33	0.98	0.00	0.00	0.00
T_NSC_{branch}	High	1.11	0.09	0.00	0.10	0.13	0.44	1.68	0.01	0.02
	Low	1.06	0.14	0.00	0.34	0.19	0.08	6.45	0.06	0.06
S_{leaf}	High	0.41	0.17	0.02	0.16	0.18	0.38	14.19	0.01	0.14
	Low	0.55	0.24	0.03	0.05	0.29	0.87	11.43	0.00	0.11
St_{leaf}	High	0.10	0.17	0.56	0.33	0.22	0.15	4.01	0.03	0.04
	Low	0.32	0.20	0.12	0.04	0.28	0.90	0.04	0.00	0.00
T_NSC_{leaf}	High	**1.01**	**0.12**	**0.00**	**0.31**	**0.13**	**0.02**	**17.72**	**0.06**	**0.18**
	Low	1.20	0.13	0.00	0.15	0.18	0.42	1.45	0.01	0.01

The responses to light and drought treatment found in Figures 1 and 2 were also consistent with the mixed effect modelling (MEM) results presented in Table 1. When accounting for the influence of taxonomic group on the intercept of our trait variables versus the drought treatment effect, V_{cmax} and J_{max} retained a significant relationship with the fixed treatment effect with conditional r^2 values of 0.15 and 0.22, respectively. The MEM analysis replicated almost all the significant effects found within Figures 1 and 2 with conditional r^2 values ranging from 0.08 to 0.24 (Table 1). However, a significant treatment effect on starch in the branches and leaves was not replicated in the MEM analysis, yielding $p \geq 0.05$. Although qualitatively these results had a model trend in the same direction as in Figure 2, in these models, significance values were 0.11 and 0.15 respectively (Table 1). We tested a mixed-effect model for the combined influence of light and plot, and their interaction on our traits, with the statistical power of these tests being weaker (Table S3).

We note that the proportion of variance explained by Genus, as the random variable in the MEMs ranged from 0% to 22% (Table 1;

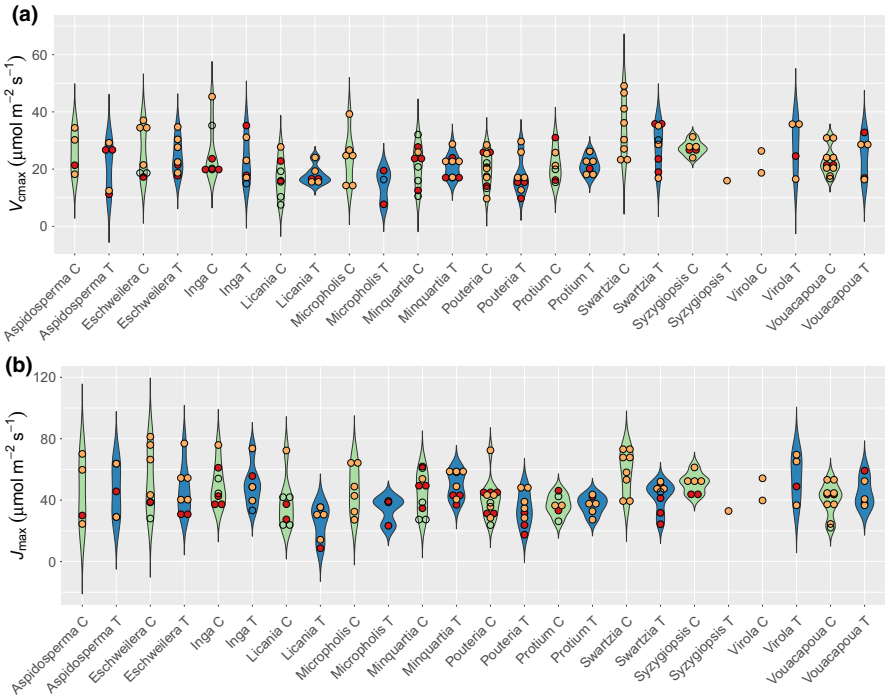


FIGURE 3 Violin plots showing variance in maximum carboxylation capacity (V_{cmax}, µmol m^{-2} s^{-1}), and maximum electron transport rate (J_{max}, µmol m^{-2} s^{-1}), standardised to 25°C, within each genus sampled on the control (C, green violins) and drought treatment (T, blue violins) trees. Points within the violin represent individual trees within each genus, coloured according to high light (categories 4 and 5, orange), low light (categories 2 and 3, red) and light category 1, which remains transparent, as it was not used within the high and low categories due to low replication (see Section 2)

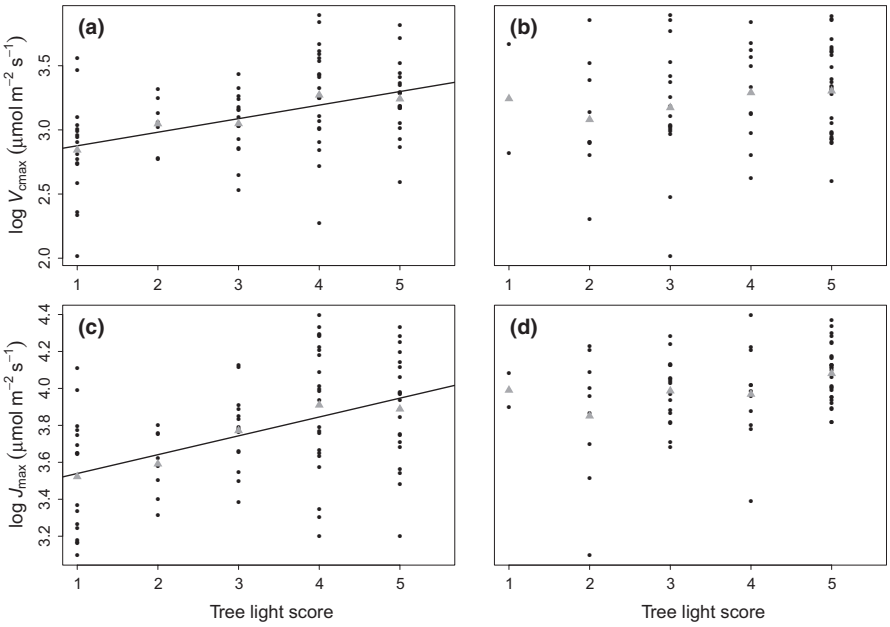


FIGURE 4 Generalised linear regression plots between maximum carboxylation capacity (V_{cmax}, µmol m^{-2} s^{-1}) and maximum electron transport rate (J_{max}, µmol m^{-2} s^{-1}), standardised to 25°C, with the ordered factor for light class. Relationships are shown for the control (a, c) and drought treatment (b, d) trees. Black points show the values per tree and grey triangles show the mean value for each light class

Table S3), however, in many cases the conditional r^2 remained substantially higher than the marginal r^2. The mixed role for genus across the significant MEM, may be explained by high trait variability within genera, as demonstrated for V_{cmax} and J_{max} (Figure 3). This same variability was also found when the analysis was repeated with species rather than genus grouping (Figure S2). Consequently using species nested within genus did not produce significantly better results than using genus alone, as genus alone either maintained the same or a lower AIC score than did species nested within genus.

The role of light in controlling V_{cmax} and J_{max} in our MEM modelling results is likely to be the consequence of a positive relationship between all light classes (1–5) with V_{cmax} and J_{max} in the control trees, which is absent on the drought treatment. When light classes 1–5 were included in a glm as an ordered factor, a significant positive linear relationship was found in the control trees (Figure 4), which was absent from the drought treatment. However, no significant quadratic, cubed or x^4 relationship was found with our ordered light factor on the control or treatment.

4 | DISCUSSION

We demonstrate that, across our relatively large sample size, down-regulation of traits controlling carbon assimilation and changes in

carbohydrate storage can occur following long-term drought-stress, but downregulation in leaf respiration rates does not occur. However, these processes are strongly affected by the full light exposure status of each tree's canopy and this becomes important to account for extended moisture stress where drought-induced tree mortality or leaf abscission can substantially increase light availability to tree crowns. We observed a significant decrease in minimum g_s and a significant increase in P_{leaf} following the altered moisture availability and light exposure imposed by the drought treatment, but these were the only traits that showed consistent adjustments across both high and low light classes on the drought treatment (Figure 1; Table 1; Table S3). Significant differences between other variables measured in the treatment and control trees appeared to be related to the light environment of the tree (Figures 1 and 2; Tables 1; Table S3). Relative to the control trees, those in the drought treatment with crowns exposed to high radiation (light scores of 4–5), as well as showing moderate decreases in V_{cmax} and J_{max}, had significantly reduced branch starch content and increased branch soluble sugars, leaf starch and total leaf NSC content. In contrast, no significant drought treatment differences in these variables were observed in trees with more shaded crowns (low light class trees, light scores 2–3; Figures 1 and 2), or on average, when all light classes were combined. This observed division in response under combined drought treatment and high light exposure may have been associated with the apparent breakdown in the relationship between canopy light class and photosynthetic capacity on the treatment, which we observe in Figure 4, although we note that this relationship is unlikely to be fully linear, as suggested by the excess positive residuals in certain light classes (Figure 4). Our analysis suggests that canopy light conditions are likely to influence functional traits and responses to drought by tropical forests.

Trees with canopies receiving high radiation loads may suffer greater stress during drought due to elevated leaf temperatures and leaf-to-air VPD. Photosynthetic acclimation to irradiance (Field & Mooney, 1986) has been found to depart from optimality towards the upper levels of forest canopies as additional ecological constraints (e.g. stomatal or non-stomatal limitations in photosynthesis) become increasingly important for the foliar carbon economy (Meir et al., 2002). The decline in the photosynthetic capacity of the drought trees receiving high light may be a consequence of a greater hydraulic cost of increasing g_s during periods when they might otherwise fully utilise elevated photosynthetic capacities (Wang et al., 2017). Although other factors may also suppress photosynthetic capacity, such as accumulation of NSC (Figure 2), it is likely that there is no net gain in maintaining high photosynthetic capacity given the hydraulic costs of opening stomata in the drought treatment when light levels are high, especially if the respiration costs of maintaining photosynthetic capacity remains unchanged.

Overall, the leaves of the drought treatment trees with high light exposed crowns had increased concentrations of starch and total NSC (Figure 2; Table 1), which may be one factor causing photosynthetic capacity to be downregulated. However, we note that when accounting for Genus in the MEM model analysis, the observed difference in leaf starch concentrations between plots (Figure 2) was no longer significant, even though the trend remained the same and the total NSC in the leaves remained significantly higher in the treatment in the MEM model (Table 1). Also accounting for genus as a random factor, may be responsible for the lack of significant results for the NSC variables within the mixed effect models which combined both light and treatment effects (Table S3), which more generally demonstrated lower statistical power. This may be indicative of the influences of genus and light on the treatment effect countering one another within our models. However, overall higher leaf NSC levels in the drought treatment trees, as suggested by Figure 2 and Table 1 may suggest that: (a) their carbon assimilation is outstripping their capacity to use it for growth or other metabolic functions (Sala & Hoch, 2009); (b) the surviving trees are actively increasing their long-term resilience to drought by building up carbon reserves (Martinez-Vilalta et al., 2016; O'Brien et al., 2014); and/or (c) drought-related phloem restrictions are limiting carbon transport out of the leaf (Mencuccini et al., 2015; Sevanto et al., 2014). The potential for increased storage of NSC as starch rather than soluble sugars in the leaves of the drought treatment trees may reflect the crucial role soluble sugars play in maintaining turgor and in osmoregulation (Bartlett et al., 2014). Storing excess carbohydrate in leaves as a build-up of soluble sugars could substantially alter plant water status (Martinez-Vilalta et al., 2016), whereas the observed increase in starch storage (Figure 2) would avoid such alterations.

It is also possible that the storage of carbohydrate as soluble sugars has different implications for water transport in branch tissue (Figure 2; Table 1) than in leaves: consistent with this, we observe a shift from branches storing more NSC as starch, to storing more NSC as soluble sugars in the drought treatment relative to the control trees. Higher soluble sugar concentrations in woody tissue may be beneficial as a survival strategy for the remaining droughted trees, as soluble sugars can be more rapidly used without requiring hydrolysis, as is needed with starch (Mencuccini & Holtta, 2010), potentially speeding up processes such as xylem repair (e.g. Secchi & Zwieniecki, 2011). Other processes, for example phloem transport to support increased allocation to roots during drought (Arndt et al., 2001), may also benefit from increased concentrations of soluble sugars in woody tissue (Savage et al., 2016). Notwithstanding our use of a narrow sampling window in the field to facilitate comparison between the drought treatment and the control (same times of day and year, and no change in weather patterns during whole sampling period), we note the need for caution in our interpretation of these data given evidence elsewhere (e.g. Tixier et al., 2018) of rapid diurnal changes in leaf and branch NSC (100% and 50% respectively). Further diurnal and seasonal monitoring would clearly strengthen our understanding of the roles and consequences of changes in NSC storage and use in different tree organs under drought.

Interestingly, the results reported here contrast with previous results from the same site, which had shown no average differences in NSC or photosynthetic capacity between the drought treatment and

the control, and an increase in R_{leaf} on the drought treatment relative to control (Meir et al., 2008; Metcalfe, Lobo-do-Vale, et al., 2010; Rowland, da Costa, Galbraith, et al., 2015; Rowland, Lobo-do-Vale, et al., 2015). Although the absolute values of photosynthetic capacity and R_{leaf} were similar for drought treatment and control trees across all these studies, here we observed differences between drought treatment and control in NSC concentrations and photosynthetic capacity (V_{cmax}, J_{max}) when trees were further distinguished by light class, but we detected no differences in R_{leaf}. We attribute the changes in photosynthetic capacity and NSC concentrations we now detect to: (a) a sampling strategy designed to capture the effect of the whole tree canopy light environment on trait variation, rather than selecting only sun-lit canopy-top branches; (b) a substantially larger sampling size and (c) a more comprehensive taxonomic coverage (162 trees, 12 genera and 32 species, vs. 42 trees, 6 genera and 10 species in Rowland, Lobo-do-Vale, et al., 2015; or 17 trees in Metcalfe, Lobo-do-Vale, et al., 2010). Our inability to replicate previous results that had shown an increase in R_{leaf} on the droughted forest may have been particularly affected by species selection. Previously, we demonstrated increased R_{leaf} in three genera that had shown elevated mortality rates under the drought treatment relative to control (da Costa et al., 2010), but as well as this earlier study being limited in taxonomic sampling we did not analyse for variation in tree size and canopy light environment, which are likely to be key, as tree stature rather than taxonomic identity has proved to be the strongest correlate with mortality risk (da Costa et al., 2010; Rowland, da Costa, Galbraith, et al., 2015), consistent with global trends in drought-related mortality (Stovall et al., 2019). The shift in results between studies points to the importance of adequate sampling within and among taxonomic groups, given the large variation we observe here (Figure 3; Figure S2), as well as to the need to account for tree crown light exposure in tropical rainforests in order to ensure robust estimates of the effects of environmental change on stand-scale processes.

Our study demonstrates that changes in tropical tree function with canopy light conditions can have a strong influence on drought responses, controlling carbon assimilation and storage rates at stand scale. Predicted long-term changes in climate require accurate estimation of mortality-driven changes in both stand density and the biophysical impacts on vegetation. Our study emphasises the need to account for forest and light-exposure dynamics in model simulations in order to understand the long-term ecophysiological performance of tropical forests.

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AUTHORS' CONTRIBUTIONS

L.R., M.M., R.S.O. and P.M. designed the data collection; A.C.L.d.C. and P.M. designed the drought experiment; L.R., A.C.L.d.C., P.R.L.B., I.C., P.d.B.C., A.G., T.F.D., R.C.M., L.V.F., S.S.V., J.A.S.J. and A.A.R.O. all contributed to data collection and all authors contributed to writing the manuscript.

DATA AVAILABILITY STATEMENT

Data have been deposited in DRYAD (Rowland et al., 2020), and are available from https://doi.org/10.5061/dryad.vdncjsxs5.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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